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NEUROCOGNITION OF MAJOR-MINOR AND CONSONANCE-DISSONANCE

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MAJOR-MINOR AND CONSONANCE-DISSONANCE ARE two profound elements of Western tonal music, and have strong affective connotations for Western listeners. This review summarizes recent evidence on the neurocognitive basis of major-minor and consonance-dissonance by presenting studies on their processing and how it is affected by maturation, musical enculturation, and music training. Based on recent findings in the field, it is proposed that both classifications, particularly consonance-dissonance, have partly innate, biologically hard-wired properties. These properties can make them discriminable even for newborn infants and individuals living outside the Western music culture and, to a small extent, reflect their affective connotations in Western music. Still, musical enculturation and active music training drastically modify the sensory/acoustical as well as affective processing of major-minor and consonance-dissonance. This leads to considerable variance in psychophysiological and behavioral responses to these musical classifications.

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MUSIC IS A UNIVERSAL PHENOMENON among human cultures, carrying emotional meaning to the majority of listeners. While almost all of us become experts in our mother tongue, not all individuals become highly proficient in producing and perceiving music. Thus, unlike language, music enables comparisons between experts and laymen to study neural plasticity and learning. The last decades in the neuroscience of music have demonstrated that music training is associated with considerable plasticity in the brain structure and function related to music processing (see; Moreno & Bidelman, 2014; Pantev & Herholz, 2011), visible already in young children after short periods of training (Kraus & Chandrasekaran, 2010). The scope of research on music processing has

even widened to infancy, and behavioral and brain studies have demonstrated many music-related auditory skills during the first months of life (Hannon, & Trainor 2007; Trainor & Corrigall, 2010; Trehub, 2010). Infants with limited exposure to music of their culture offer an opportunity to study the earliest skills for music processing, serving as candidates for innate universal abilities which all music cultures build on.

According to present understanding, the development of music processing is based on, first, early auditory skills that serve as building blocks for music processing, and second, the process of musical enculturation that leads to facilitated processing of music of one's own culture due to exposure without explicit training (Hannon & Trainor, 2007). This development is modified by several individual factors such as musical aptitude, cognitive abilities, and motivation, extending far beyond the scope of the present review. Understanding the relative contributions of biologically hard-wired auditory skills, brain maturation, enculturation, and explicit training in emotional and cognitive aspects of music processing is a future challenge in the field.

Various aspects of music have been studied in neurosciences of music, ranging from rhythm, beat, and tempo to pitch, timbre, melody, harmony, and syntax (for reviews, see Koelsch, 2011; Peretz & Zatorre, 2005). Recently, experimental paradigms enabling the investigation of various acoustic and musical features at once have been introduced and used with child and adult participants (Putkinen, Tervaniemi, Saarikivi, de Vent, & Huotilainen, 2014; Tervaniemi, Huotilainen, & Brattico, 2014; Vuust, Brattico, Seppänen, Näättänen, & Tervaniemi, 2012). Additionally, music emotions and aesthetics have received considerable interest (Brattico & Pearce, 2013; Eerola & Vuoskoski, 2012; Koelsch, 2010, 2014). Many of these studies concern development of music processing or effects of musical expertise on the brain, but they often also can relate to the question of the origins of music. While cross-cultural and cross-species studies offer another view to these questions, evidence in this field is still sparse (for a recent review, see Patel & Demorest, 2013; for a review on cross-cultural studies on music emotions see Thompson & Balkwill, 2010).

The present review will upgrade these approaches by focusing on the essential classifications of major-minor

and consonance-dissonance in the context of Western music. Defined by mutual pitch relationships between simultaneous or consecutive tones, they are at the heart of the spectral dimension of Western music. They are low-level acoustic phenomena that can be studied in controlled experiments even in infants. Still, these classifications have cultural relevance and affective meaning to Western listeners. Novel findings in music neuroscience and psychology on the universal aspects of music-evoked emotions, earliest auditory skills for music processing, and the neural basis of dissonance have shed light on the origins and development of major-minor and consonance-dissonance. Brain research and behavioral findings, reaching across different age groups, cultures and species are reviewed in order to discuss the roles of biology, brain maturation, musical enculturation, and music training in major-minor and consonance-dissonance processing. The main questions in the scope of this review are: (1) what is the neurobiological basis and psychoacoustic origin of major-minor and consonance-dissonance, and (2) how do development, musical enculturation, and music training/expertise modify their affective and cognitive processing?

Major-Minor Dichotomy in Western Music

The dichotomy of major vs. minor is the basis of Western tonal music, present in scales, keys, intervals and chords. The difference between major and minor mode is rooted in the interval structures (i.e., mutual pitch relationships between simultaneous or consecutive notes in the diatonic scale), particularly the position of two semitones of the diatonic scale in the two modes. For instance, in the major mode, there is a semitone between steps 3 to 4 vs. steps 2 to 3 in the minor mode. Thus, the interval from the tonic to the third step is larger in major mode than in minor mode. Consequently, the chord structures differ as well: a major third interval in major chords is replaced by a minor third interval in minor chords (Helmholtz, 1887/1954; Rossing, Moore, & Wheeler, 2002). Examples of major and minor triad chords are presented in Figure 1. Western listeners associate affective connotations of brightness and joy with major mode, and sadness or calmness with minor mode (Crowder, 1984, 1985; Hunter, Schellenberg, & Schimmack, 2010; Khalfa, Schön, Anton, & Liegeois-Chauvel, 2005).

AFFECTIVE PROCESSING OF MAJOR VS. MINOR

In Western adults, music in minor compared to music in major elicits more activation in brain areas related to

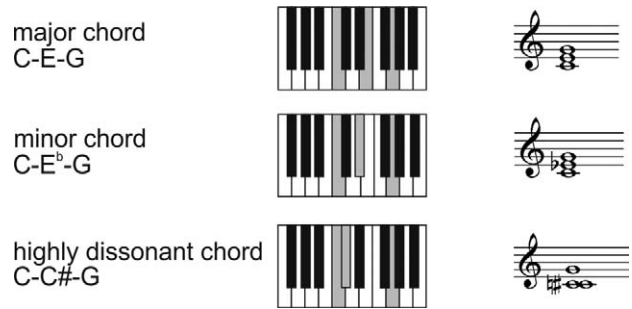


FIGURE 1. Examples of major, minor, and dissonant interval structures illustrated on a piano keyboard and in musical notation: C major triad, C minor triad, and a highly dissonant triad chord constructed of two dissonant intervals, minor second and tritone. Modified from Virtala (2015).

emotion processing; for example parts of cingulate cortex and left medial and frontal gyri (Green et al., 2008; Khalfa et al., 2005), left parahippocampal gyrus (Green et al., 2008), as well as amygdala, retrosplenial cortex, brain stem, and cerebellum (Pallesen et al., 2005; for recent reviews on the neural basis of music-evoked emotions, see Koelsch, 2010, 2014). Compared to neutral music, major and minor music both have elicited activation in the inferior frontal gyri as well as anterior cingulate cortex and medial thalamus (Mizuno & Sugishita, 2007). Experimental stimuli in the study consisted of piano chord sequences with only major chords (rated by the participants as “cheerful”), only minor chords (rated as “sad”), or various chord types (major, minor, augmented, and diminished; rated as “neutral”). Other studies presented melodies played on a piano (Green et al., 2008; Khalfa et al., 2005) or individual piano chords (Pallesen et al., 2005). Importantly, in all of the aforementioned studies, tempo was kept constant between major and minor stimuli and thus cannot explain the obtained results. Various other musical features and the surrounding music context are highly likely to influence the affective responses to major and minor music in natural listening situations. For example intensity and rhythmic elements of music make it dynamic by accenting certain events and dampening others. In order to understand their contributions for affective major-minor processing, more research is needed, where these features are not only controlled for, but experimentally manipulated.

In an fMRI study, where minor, major, and highly dissonant (chromatic scale of uniformly distributed dissonant intervals) melodies were presented to Western nonmusicians, emotion-related limbic activation elicited by the minor mode melodies was stronger than that elicited by major melodies, and only partly overlapped

with the activity elicited by dissonant melodies (Green et al., 2008). The researchers concluded that the differential affective connotations of major and minor are not merely attributable to the dissonance of the minor, as has been suggested in psychoacoustics of music (Crowder, 1984; Helmholtz, 1887/1954). However, the interpretation of the result is complicated by the learned differential affective connotations of minor vs. dissonant music in Western individuals. While brain research speaks for the strong and differing affective connotations of major and minor music for Western listeners, these studies cannot shed light on their more universal psychoacoustic or evolutionary origins.

DEVELOPMENT OF AFFECTIVE MAJOR-MINOR PROCESSING

Western children demonstrate accurate categorization of major and minor melodies based on affective labeling happy/sad after age five years but usually not before that. Three- to five-year-olds, unlike older children and adults, failed to show adequate happy/sad labeling in several studies with similar protocols (Dalla Bella, Peretz, Rousseau, & Gosselin, 2001; Gerardi & Gerken, 1995; Gregory, Worrall, & Sarge, 1996; however, see Kastner & Crowder, 1990). Nieminen and colleagues (Nieminen, Istok, Brattico, & Tervaniemi, 2012) showed that accurate rating of major melodies as happy and minor melodies as sad by 8- and 9-year-olds was preceded with children 6 years and older *preferring* major over minor melodies. Still, in one behavioral study, Western infants failed to demonstrate any preference between major vs. minor chords, as indicated by their similar looking times towards sound sources presenting major vs. minor chords (Crowder, Reznick, & Rosenkranz, 1991). However, chord processing may be a more challenging task than melody processing because melodies offer more information and processing time to the listener. Furthermore, as discussed below, in the auditory preference paradigm cognitive and affective processing of stimuli are intertwined.

The reviewed findings suggest that minor mode's affective connotation would mostly be the learned (and arbitrary) cultural association of minor mode with sad affect, and thus it would be due to familiarity (for a review, see Nieminen, Istok, Brattico, Tervaniemi, & Huotilainen, 2011). However, immature socioemotional and cognitive development in childhood might restrict the ability to make affective judgments (of music), even if the judgment lies on universal affective cues. This ability still seems to be present earlier in development than the skill to set adequate affective labels on major and minor modes, as illustrated by the tendency to use tempo as an affective cue in music before mode (Dalla

Bella et al., 2001; Mote, 2011). Notably, tempo is used as an affective cue in music also cross-culturally, suggesting a more straightforward universal basis to tempo than mode processing (e.g., Balkwill & Thompson, 1999). Tempo may dominate valence judgments over mode also in Western adults (Khalfa et al., 2005). In a music context, it is likely to interact with mode processing in a rich and complex manner. For example, 5-year-olds adequately judge a piece happy when the music has both major mode *and* fast tempo (Hunter, Schellenberg, & Stalinski, 2011).

Additional evidence for affective music processing prior to affective major-minor processing comes from infants' tendency to recognize/differentiate between happy and sad music (although this result is not very conclusive; Nawrot, 2003), and infants' ability to express preferences for consonant compared to dissonant music (see next section). However, even if major-minor processing is not restricted by affective development, it is most likely restricted by perceptual development: the child's ability to process pitch and harmony in complex tones. There are not many well-controlled experimental studies on affective judgments of major vs. minor music in small children and infants, possibly due to methodological challenges in behavioral studies (for some recent studies on affective music processing of small children see, e.g., Flom, Gentile, & Pich, 2008; Stachó, Saarikallio, van Zijl, Huotilainen, & Toivainen, 2013). Brain research on the affective processing of major vs. minor mode as well as other music elements in infants and children would be beneficial in shedding light on their early development.

UNIVERSAL COMPONENTS IN THE AFFECTIVE LABELS?

The affective judgments of music in major vs. minor mode have also been studied cross-culturally. A pioneering study by Fritz and colleagues (2009) showed that both Western listeners and members of an African Mafa tribe naïve to Western music mostly rated major music as happy (rather than sad or scared/fearful), although the tendency was stronger and more consistent among Western listeners. Experimental stimuli were computer-generated piano pieces and excerpts of natural instrumental music pieces. However, these kinds of cross-cultural comparisons are extremely difficult to conduct and interpret due to differences in how familiar the participants are with the testing settings, how they interpret the given task instructions, and the increasing challenges of finding human populations truly unreached by Western music culture. The aforementioned study by Fritz and colleagues (2009) is among the few to investigate such a population. Some

issues still compromised the obtained results. For example, pictures of facial expressions of a Western white female were presented as response options, which is not necessarily a culture-free way to study emotional judgments. Also, in the presented music pieces, many features varied at the same time (mode, tempo, pitch range, tone density, and rhythmic regularity) and the pieces were not designed to study major-minor processing per se (e.g., apparently tempo often correlated with mode). Because of this, the study by Fritz and colleagues should not be treated as conclusive evidence of universal affective processing of Western music mode, but more research is needed.

Another line of studies demonstrating a more objective estimation of the affective connotations in music cross-culturally was conducted by Bowling, Sundararajan, Han, and Purves (2012), who demonstrated that the tonal relationships in Western major and minor music are very similar to South Indian music, with corresponding affective connotations, and that the same affective correspondences are seen between the vocalizations of Western English and South Indian Tamil languages (see also Bowling, Kamraan, Choi, Prinz, & Purves, 2010). These observations point to the direction of at least partly acoustical, biological origins of major-happy, minor-sad connotations, and interestingly link them to the evolution of the human speech system (suggesting that music imitates human voice; for a review, see Bowling, 2013; for similarities between affective cues in vocal expressions and music, see also Juslin & Laukka, 2003).

Recently, Parncutt (2014) introduced an extensive list of possible origins for the affective connotations of major and minor tonalities that have been discussed in the course of Western music history. At least three of his suggestions seem to get support or opposition from the aforementioned studies, namely, *the dissonance hypothesis*, *the familiarity hypothesis*, and *the speech hypothesis*. According to the dissonance hypothesis, a higher level of sensory dissonance in the tonal relationships of minor compared to major would explain the affective connotation of minor mode. Dissonance seemed insufficient to explain the affective connotation of minor music for Western listeners in the fMRI study by Green and colleagues (2008). However, this cannot be considered as convincing evidence against the dissonance hypothesis, since the participants had experience in Western music and thus the differential affective connotations of minor and dissonant music.

The familiarity hypothesis suggests that the affective connotations of major and minor modes arise from learned associations. Support for it is offered by Western children requiring a certain amount of exposure to

major and minor music, i.e., familiarization with their affective connotations, before they can make adequate affective judgments on them (Dalla Bella et al., 2001; Nieminen et al., 2011). Still, the possibility remains that affective major-minor processing in childhood is restricted by perceptual development rather than lack of musical enculturation. On the contrary, members of the African Mafa tribe—unfamiliar with Western music—seemed to recognize the affective connotations of major and minor music to some extent (Fritz et al., 2009), although the evidence is not conclusive for reasons discussed above. Finally, the speech hypothesis of Parncutt (2014) links the lower than expected pitch of minor music with the lower-than-expected pitch of sad speech, in line with the findings of Bowling and colleagues (2010, 2012, 2013). Based on the speech hypothesis, affective connotations of major vs. minor are related to their specific psychoacoustic features. Because these features are universal to some extent, according to the hypothesis, the affective connotations of major-minor dichotomy are also likely to have a certain degree of universality.

Current evidence gives a very vague answer to the question of whether the affective connotations of major vs. minor have an innate, universal component. Even when present, the universal component is likely to be buried under a large pile of cultural influences and personal experiences that largely determine how music is perceived and which emotions are evoked. In a recent more general study on cross-cultural performance and perception of affective expression in music, basic emotions intended by performers were accurately recognized by the listeners universally, but more so when the music was from the listeners' own culture (Laukka, Eerola, Thingujam, Yamasaki, & Beller, 2013). Thus, while it is evident that there are some universally shared emotional cues in music (possibly shared with speech), enculturation still modifies affective music processing. Interestingly, comparing the affective judgments and physiological reactions of Canadians and Congolese Pygmies while listening to Western music excerpts (orchestral and film music) or recordings of vocal Pygmy music demonstrated that the physiological reactions and subjective responses to the arousal level of music were more similar across cultures than valence judgments (Egermann, Fernando, Chuen, & McAdams, 2014). Both Western and Pygmy listeners rated their own culture's music as more arousing than the other culture's music, again suggesting that familiarity and enculturation have a large role in affective processing of music. When Western listeners judged Western music as arousing, Pygmies also responded with increased physiological arousal

(Egermann et al., 2014). Recording physiological in addition to behavioral responses to music may give important additional information in cross-cultural studies on (affective) music perception.

The issue of innateness or universality in major-happy, minor-sad associations is further complicated by the fact that emotional and aesthetic judgments of major and minor music even among Western listeners are far from straightforward. They depend on, for example, the listeners' mood: sad listeners do not show the typical preference of major over minor music (Hunter, Schellenberg, & Griffith, 2011). While Western listeners usually give higher liking-ratings to major vs. minor music, higher happy-ratings to major vs. minor music and higher sad-ratings to minor vs. major music, their emotional judgments and preferences are affected by both personality and the amount of music training (Ladinig & Schellenberg, 2012; Vuoskoski, Thompson, McIlwain, & Eerola, 2012). For example, higher levels of music training are associated with higher liking ratings for music that evokes both happy and sad feelings (i.e., that is emotionally less obvious; Ladinig & Schellenberg, 2012). Interestingly, an fMRI study did not find differences between musicians and nonmusicians in emotion-related brain activity to major vs. minor chords, while the affective judgments were pronounced in musicians (they rated minor chords as sadder than nonmusicians, Pallesen et al., 2005).

Also, it is noteworthy that music in minor mode is often liked and considered beautiful and pleasant by music experts as well as laymen (Brattico et al., 2016). A recent study demonstrated that listening to sad music can evoke either positive or negative emotions due to various reasons (Eerola & Peltola, 2016). Thus, recognizing the sad affective connotation of minor mode does not necessarily imply judging it unpleasant or disliked (see also Vuoskoski & Eerola, 2012). Neither is the range of music-evoked emotions restricted to happy/sad or liked/disliked dichotomies, but it has a much richer spectrum (see, e.g., Eerola & Vuoskoski, 2012).

SENSORY/ACOUSTICAL DISCRIMINATION OF MAJOR FROM MINOR

Familiarity with the affective connotations may make it easier for the listener to discriminate between major and minor music. Without the cue to utilize affective connotations in major-minor categorization tasks, discriminating between major and minor melodies can be difficult for Western adults and improve when advised to use affective labelling (Halpern, Bartlett, & Dowling, 1998; Halpern, Martin, & Reed, 2008; Leaver & Halpern,

2004; however Crowder, 1985, obtained contrasting results with sinusoidal chords). Thus, it can be stated that the affective dichotomy of happy, bright, etc. vs. sad, peaceful, etc., is more easily mastered by human listeners than the acoustical, sensory discrimination between major and minor *per se*. On the other hand, when children were taught to describe melodies with terms "major" and "minor" *without* affective labelling, 5-year-olds already performed quite well in identifying mode changes (Costa-Giomi, 1996). Readiness to discriminate between the interval structures, i.e., acoustical differences between major and minor modes seemed to appear earlier in development than the ability to associate major and minor with their affective connotations and make affective judgments of them. In Western adults, when the affective connotations have already been acquired, they can support the categorization of major and minor modes. Certainly the sensory discrimination of minor from major mode is still a prerequisite for their adequate affective processing: without being able to perceptually discern two stimuli, it is impossible to associate different affective labels with them. This does not rule out the possibility that familiarity with the affective labels may then further support differentiation of the stimuli.

MAJOR-MINOR CATEGORIZATION IN WESTERN LISTENERS

In order to empirically study the acoustical categorization of major vs. minor in Western music, it is beneficial to minimize the presence of other musical elements (like tempo) in order to gain maximal experimental control. Accordingly, studying neural instead of behavioral responses makes it easier to compare the same processes in children and adults as well as musicians and nonmusicians without confounding factors of attention, task familiarity, or motivation. In recent years, the MMN response (mismatch negativity) has been largely utilized for this purpose. It reflects neural difference between expected and encountered sound (for reviews, see Kujala, Tervaniemi, & Schröger, 2007; Näätänen, Paavilainen, Rinne, & Alho, 2007; Näätänen, Tervaniemi, Sussman, Paavilainen, & Winkler, 2001; Tervaniemi & Huotilainen, 2003). It has been recorded in passive listening conditions with electroencephalography (EEG) and magnetoencephalography (MEG) to study preattentive discrimination of single major and minor chords presented without a music context in adults (Brattico et al., 2009; Tervaniemi, Sannemann, Nöyränen, Salonen, & Pihko, 2011; Virtala et al., 2011; Virtala, Huotilainen, Partanen, & Tervaniemi, 2014) and children (Putkinen, Tervaniemi, Saarikivi, Ojala, & Huotilainen, 2014; Virtala, Huotilainen, Putkinen, Makkonen,

& Tervaniemi, 2012) with and without formal music training, as well as newborn infants (Virtala, Huotilainen, Partanen, Fellman, & Tervaniemi, 2013).

The MMN studies on major-minor processing have demonstrated that Western adults demonstrate a sensitivity to the difference between major and minor chords regardless of their formal music training background (Brattico et al., 2009; Tervaniemi et al., 2011), while musicianship facilitates the discrimination (Tervaniemi et al., 2011). School-aged children demonstrated MMNs to minor chords among major chords, and the responses grew larger with age, suggesting improved processing of the dichotomy (Putkinen et al., 2014a). The group with music training demonstrated a steeper increase in their MMN amplitudes with age than the control peer group with other hobbies (Putkinen, Tervaniemi, Saarikivi, Ojala, & Huotilainen, 2014). Taken together, the results demonstrate preattentive readiness for major vs. minor chord categorization in Western children and adults with and without formal music training, and facilitating effects of both musical enculturation (increasing age indicates increasing exposure to Western music) as well as music training and expertise on chord processing.

All of the aforementioned MMN-studies on major-minor processing were, however, conducted with highly repetitive oddball paradigms, where only one major chord (from one frequency level) was presented and occasionally replaced by one minor chord. It is possible that MMN is elicited in these studies as a response to the new frequency in the minor chord, instead of the chord being a minor chord. Furthermore, unnatural paradigms lack ecological validity. In order to extend and verify the findings obtained in the prior studies, Virtala and colleagues (2011) introduced a complex, abstract modification of the above-described chord paradigm. In the new design, several chord types were presented and transposed to several frequency levels, so that all the frequencies in the occasional deviant chord types were already present in the repeating standard chord type (major chord), and the only feature varying between the standard and deviant chord types was the interval structure that separates the chords by definition. In this way, MMNs could not be elicited by a novel frequency in the deviant chords unlike in previous work (Brattico et al., 2009; Putkinen, Tervaniemi, Saarikivi, Ojala, & Huotilainen, 2014; Tervaniemi et al., 2011). Also, the sound sequence was made more varying and thus more natural compared to earlier studies. The chords from all possible frequency levels within an octave followed each other randomly in the sequence, and thus no key was established.

Figure 2 illustrates the experimental paradigm and results by Virtala and colleagues (2011, 2012, 2013, 2014). When presented with the new chord paradigm, nonmusician adults still demonstrated MMNs to minor chords among major chords (Virtala et al., 2011). Music expertise facilitated this processing both at the neural level of MMN elicitation and at the behavioral level, in a listening task where the deviant minor chords had to be detected from a stream of repeating randomly transposed major chords (Virtala et al., 2014). By school age, major-minor discrimination was already facilitated in children with music training compared to children with non-music-related hobbies: only the musically trained children demonstrated MMNs to the major-minor contrast (Virtala et al., 2012). Also, when the music background of the nonmusician adults was strictly controlled (limited to a maximum of two years of any music training during lifetime), the nonmusicians no longer showed evidence of mode discrimination in the preattentive level of MMN elicitation, and their performance was poor also in the behavioral level (Virtala et al., 2014). The results are in line with an earlier study where nonmusicians were able to discriminate major from minor chord arpeggios above chance, but musicians were clearly superior in the task, and the group difference was evident also in subcortical encoding of the stimuli (Bidelman, Krishnan, & Gandour, 2011).

Overall the results by Virtala et al. (2011, 2012, 2014) demonstrate a facilitating effect of music expertise on chord discrimination in the preattentive level of MMN elicitation both in children and adults. The findings suggest that the differential neural representations of major and minor chords may be less fine-grained when resulting from musical enculturation instead of formal, explicit training. However, it is notable that all the aforementioned studies only cover the categorization of individual major vs. minor triad chords. In a music context with chord cadences or major vs. minor scales instead of chords, processing this dichotomy is likely to be different (probably facilitated because there are more acoustic cues). This should be examined in future studies.

MAJOR-MINOR CATEGORIZATION IN INFANCY

Crowder and colleagues (1991) found no evidence for preference of major over minor mode in Western infants, unlike what is seen in older children (e.g., Nieminen et al., 2011, 2012). Direction of gaze towards the sound source and the looking time were measured as indices of auditory preference for major vs. minor chords in infants (Crowder et al., 1991), while older children were asked to rate music pieces according to how much they liked them (Nieminen et al., 2012). The

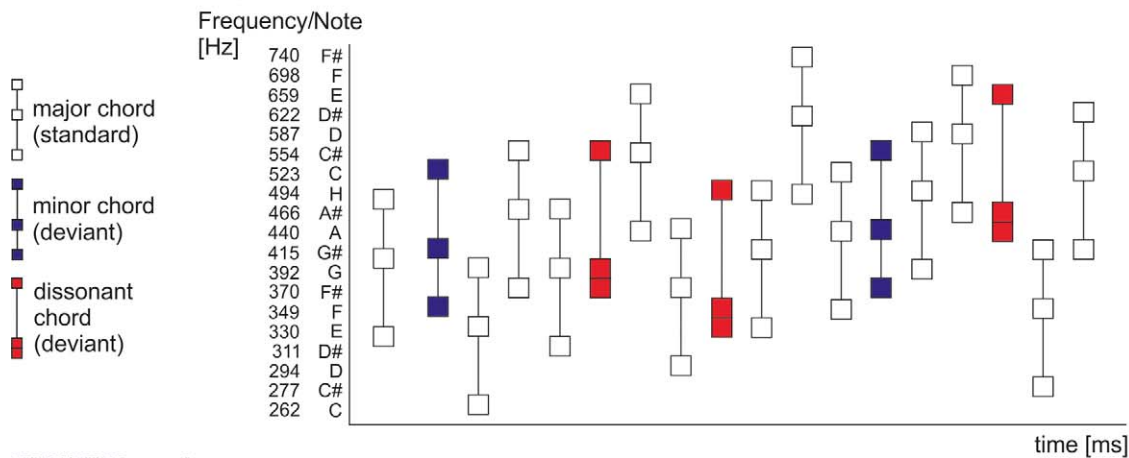
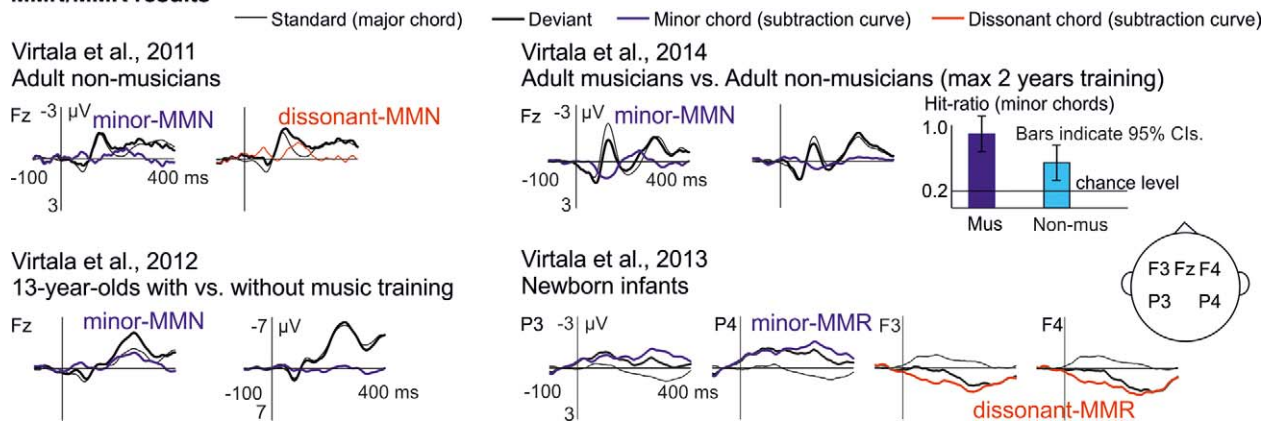
Experimental paradigm**MMN/MMR results**

FIGURE 2. Experimental paradigm and results of the MMN studies on major-minor and consonance-dissonance chord processing by Virtala et al., 2011, 2012, 2013, and 2014 (data replotted). All studies additionally included second inversions of major chords as deviant stimuli, not presented here. Newborn equivalents of MMN are termed mismatch responses (MMRs). Modified from Virtala (2015).

auditory preference may or may not reflect affective processing of the presented sounds (for a discussion, see Nieminen et al., 2012). However, the ability to prefer a sound over another at least requires that the sounds can be perceptually discriminated. An early readiness to discriminate between major and minor modes would offer evidence that the dichotomy would be to some extent rooted in the innate properties of the human auditory system.

In order to further explore the roles of early, innate auditory skills (nature) and musical enculturation (nurture) in major-minor discrimination, the chord paradigm of Virtala and colleagues (2011) was presented to Western newborn infants (Virtala et al., 2013). The MMN response can be recorded from newborn infants during sleep, and thus offers a unique possibility to study early auditory readiness independent of infants' behavioral reactions (Kujala et al., 2007). Surprisingly,

the minor chords did elicit mismatch-like responses in the context of major chords in neonates. However, the obtained response was statistically significant only on one parietal electrode site. Furthermore, it seemed to contrast with the earlier finding that 13-year-olds without music training did not demonstrate MMNs to minor among major chords (Virtala et al., 2012). The result, although novel and tentative, is in line with a body of research on infants' complex and music-related auditory skills, demonstrating the ability to process small pitch changes and relative pitch (Alho, Sainio, Sajaniemi, Reinikainen, & Näätänen, 1990; Chang & Trehub, 1977; Plantinga & Trainor, 2005; Stefanics et al., 2009; Tew, Fujioka, He, & Trainor, 2009; Trehub, Cohen, Thorpe, & Morrongiello, 1986) and sensitivity to changes in interval width between tone pairs (Stefanics et al., 2009; Tew et al., 2009). However, although music-related, these phenomena are not specific to music. For

example, relative pitch is needed in speech as well as music perception. Also, it is noteworthy that musical enculturation is likely to start as early as in utero (see, e.g., Partanen, Kujala, Tervaniemi, & Huotilainen, 2013)—not even a newborn is a music cultural “*tabula rasa*.”

To conclude, (affective) processing of major-minor is challenging to study in an age- and culture-sensitive manner. This makes it difficult to make conclusions on their origin. In the future, it may be informative to study cross-cultural as well as early childhood’s affective processing of music with psychophysiological in addition to behavioral methods. While physiological or neural responses only partly reflect what the person is thinking or feeling, they are also less likely to include error due to factors like motivation, attention, or differential interpretation of task instructions. One of the first attempts to this direction is the study by Virtala and colleagues (2013), offering pioneering evidence that early auditory skills of newborns may generalize to preattentive discrimination of major and minor triad chords in a context with varying frequency. Together with results presented above, demonstrating acoustical similarities between sad music and sad speech from different cultures (Bowling, 2013; Bowling et al., 2010, 2012), it is probable that major vs. minor dichotomy and its affective connotations partly build on universal acoustical properties. Still, it is obvious that musical enculturation, music training, and expertise facilitate the neural representations of major vs. minor and also modify their affective processing, e.g., towards more precise judgments on familiar than unfamiliar music.

Consonance-Dissonance in Western Music

Sensations of consonance and dissonance are rooted in frequency combinations of simultaneously played tones and their overtones (reviewed in Bidelman, 2013; Helmholtz, 1887/1954; Krumhansl, 1990; Parncutt & Hair, 2011; Plomp, & Levelt, 1965; Rossing et al., 2002). Figure 1 illustrates a dissonant chord constructed of two intervals considered highly dissonant in Western music: a minor second and a tritone. While small-integer frequency ratios, e.g., 4:5 in a major third interval, tend to sound consonant, large-integer frequency ratios, e.g., 15:16 in a minor second, sound dissonant. The essence of consonance vs. dissonance has been attributed to this simplicity vs. complexity of frequency ratios between sounds (Helmholtz, 1887/1954; Rossing et al., 2002), and building on the frequency ratios, *beating*, slow periodic fluctuation in the amplitude of the sound wave, due to small frequency differences between the fundamental

frequencies or overtones of the simultaneously played sounds, leading to perceptual roughness (Helmholtz, 1887/1954). Plomp and Levelt (1965) suggested that if the fundamental frequencies or overtones of the simultaneously played sounds lie sufficiently far apart but within a critical band on the basilar membrane of the inner ear, their amplitude envelopes overlap in the membrane, leading to a stronger sensation of roughness and dissonance.

More recently, McDermott, Lehr, and Oxenham (2010) demonstrated that consonance perception was rather related to *harmonicity*; namely, how closely the fundamental frequencies and overtones of the simultaneously played sounds match simple harmonic proportions (of the fundamental frequencies), i.e., belong to one harmonic series. This would explain why a sensation of dissonance has emerged also in dichotic listening settings, where the dissonant interval is created by one tone presented to one ear and another tone presented to the other ear, and thus no inner ear mechanism can explain the perception of dissonance (e.g., Bidelman & Krishnan, 2009). Furthermore, this hypothesis is supported by the result that individuals with amusia do demonstrate a preference for stimuli without beating, but no preference for harmonic over inharmonic tones or consonant over dissonant music (Cousineau, McDermott, & Peretz, 2012).

In music, consonance-dissonance is a continuum that varies with time and culture, and its processing is affected by the surrounding musical context (Rossing et al., 2002). Rather than pleasant, pure consonance can be considered uninteresting in a music context (or even less pleasant than mild dissonance; see Lahdelma & Eerola, 2016, discussed below), and different music genres have different views on the use of dissonant intervals. Furthermore, Terhardt (1984) differentiated between *sensory consonance*, “the graded absence of annoying factors,” a psychoacoustical phenomenon of sounds not specific to music, and *harmony*, the music-specific component of consonance (see also Tramo, Cariani, Delgutte, & Braida, 2001). Terhardt (1984) noted that while experiments presenting individual chords mostly cover the sensory aspect of consonance, “in musical context, obviously the component ‘harmony’ prevails.” Thus, a rough distinction can be made between harmony in a musical context and sensory consonance vs. dissonance in simultaneous sounds, e.g., in chords. While both conceptions are of interest for the neuroscience of music, the latter concept of sensory consonance can be considered a lower-level psychoacoustic phenomenon, serving as the neurocognitive basis for more complex musical processes like (Western

music) harmony. To this end, the concept of sensory consonance in relation to biology and musical enculturation is reviewed below.

AFFECTIVE CONNOTATIONS OF SENSORY CONSONANCE-DISSONANCE

Sensory dissonance is defined as rough, unpleasant and unstable, whereas consonance is defined as smooth, harmonious, and stable (reviewed in Rossing et al., 2002). Thus, like major-minor categorization, the consonance-dissonance continuum also carries affective connotations in music, and the connotations may have a more biological basis than in the case of major-minor distinction. In Western adults, consonant (pleasant) and dissonant (unpleasant) music have been found to elicit differential activation patterns in brain structures including the hippocampus, parahippocampal gyrus, amygdala, temporal poles, anterior insula, and the ventral striatum (reviewed by Koelsch, 2010, 2014; see also Blood, Zatorre, Bermudez, & Evans, 1999; Gosselin et al., 2006; Khalfa et al., 2005; Koelsch, Fritz, von Cramon, Müller, & Friederici, 2006; Sammler, Grigutsch, Fritz, & Koelsch, 2007).

A GENERALIZED PREFERENCE FOR CONSONANCE?

Unlike in the case of major vs. minor modes, several behavioral studies have demonstrated that small infants already may demonstrate preference of consonant over dissonant intervals and melodies (Crowder et al., 1991; Trainor & Heinmiller, 1998; Trainor, Tsang, & Cheung, 2002; Zentner & Kagan, 1998), possibly independent of whether they have heard music in utero, as evidenced by a study on infants of deaf mothers (Masataka, 2006; it is still likely that even these infants have some prenatal music exposure). However, a recent study compromises the prior results. By recording looking times of 6-month-old infants to melodies presented in many of the previous studies (Masataka, 2006; Trainor & Heinmiller, 1998; Zentner & Kagan, 1998), Plantinga and Trehub (2014) found no evidence of preference for consonant over dissonant melodies. Independent of consonance-dissonance of the melodies, infants seemed to prefer the melodies that they had heard before during the experiment. Thus, preference for familiar rather than consonant melodies seemed to describe their affective music processing.

Considering the difficulties in conducting behavioral experiments on infants and interpreting their responses as listening preferences, different studies are likely to give different answers to the question of infants' consonance preference also in the future. Also, even when consonance preference is demonstrated in Western

infants, it can hardly be interpreted as proof of the preference being a musical universal, due to learning caused by fetal exposure to Western music conventions (Partanen et al., 2013). Rather, it can be considered more general evidence of cognitive and/or emotional abilities of infants related to music processing. Again the question also remains whether auditory preference can be interpreted as affective processing (see above). So far the authors are aware of only one brain study on affective processing of consonance vs. dissonance in infancy. An fMRI study demonstrated that in Western newborn infants, differential patterns of brain activation in emotion-related areas are elicited by consonant vs. dissonant music, suggesting differing affective connotations (Perani et al., 2010).

There is contrasting evidence of whether other species prefer consonance, and the results may depend on the species studied. While two recent studies showed no preference of consonant over dissonant intervals in tamarin monkeys (McDermott & Hauser, 2004) or Campbell's monkeys (Koda et al., 2013), one study demonstrated preference for consonant over dissonant music in a young chimpanzee with limited prior exposure to music (Sugimoto et al., 2010), and, furthermore, preference for consonant melodies over dissonant melodies has been observed in chicks (Chiandetti, & Vallortigara, 2011). Snowden and Teie (2013) review a large set of studies on emotional features in vocalizations across species. They proposed that similar features are present in music emotions, by stating that dissonant-consonant intervals in both speech and music are derived from and related to threat (complex sounds) vs. affection (pure sounds) in primitive affective vocalizations (Snowden & Teie, 2013). Thus, whether or not other species demonstrate consonance-preferences when introduced with human music, there would still be shared acoustical features between human and non-human emotional sounds.

Whether consonance preference is a human universal also remains unsolved (Butler & Daston, 1968; Fritz et al., 2009; Koelsch et al., 2006; Maher, 1976; McDermott, Schultz, Undurraga, & Godoy, 2016). A native African population naïve to Western music seemed to prefer consonance over dissonance in Western music, but the presented dissonant excerpts were also spectrally more complex than the consonant excerpts (Fritz et al., 2009), and complexity is a universal affective cue in music per se (e.g., Balkwill & Thompson, 1999). Preference for consonance was also pronounced in Western listeners (actually for both Western and Mafa music; Fritz et al., 2009). Similarly, Indian listeners judged dissonant sounds to be less "in need of resolution" than Canadian listeners,

suggesting that culture had influenced their conceptions of consonance (Maher, 1976). A very recent comparison of an Amazonian society with populations in Bolivia and the United States supports these results: the less the participants had experience with Western music harmony, the less they demonstrated a preference of consonance over dissonance (McDermott et al., 2016). Preference for consonant over dissonant chords was nonexistent in the Amazonian population with minimal exposure to Western culture and music and, apparently, no harmony in their own music culture (McDermott et al., 2016). Still, the members of this population did dislike roughness and seemed to prefer larger over smaller interval ratios. These results emphasize the role of musical enculturation and suggest a rather small universal component in how adult listeners make affective judgments of consonant vs. dissonant intervals.

AFFECTIVE CONSONANCE PROCESSING IN WESTERN MUSICIANS AND NONMUSICIANS

The effect of musical expertise on affective processing of consonance-dissonance has not received a lot of attention in research. Consonance preference seems to increase with growing amounts of formal music training in Western listeners (McDermott et al., 2010), and dissonant melodies are associated with more unpleasant emotions (Pallesen et al., 2005; Schön, Regnault, Ystad, & Besson, 2005) and stronger physiological reactions in musicians compared to nonmusicians (Dellacherie, Roy, Hugueville, Peretz, & Samson, 2011). However, in a recent study, increased familiarity with chords (learning to match the pitch of one given target note in dissonant chords with a probe tone) greatly reduced the perceived unpleasantness of the chords (McLachlan, Marco, Light, & Wilson, 2013). This is counterintuitive in light of the above-mentioned results, since musicians are likely to be much more familiar with dissonant as well as consonant intervals and melodies than nonmusicians. Also, musicians' strong negative responses towards dissonance may be considered a surprising phenomenon *per se*, since musicians are known to appreciate mixed emotions in music (Ladinig & Schellenberg, 2012). However, musicians also become highly familiar with the conventional affective connotations of different musical features and are likely to be more aware of them than nonmusicians. This may explain their pronounced reactions towards dissonance when instructed to make affective judgments.

In a recent study, both Western musicians and non-musicians actually deemed mildly dissonant (minor and

major ninth and major seventh) chords as *more pleasant* than consonant chords (Lahdelma & Eerola, 2016). Musical experts compared to laymen tended to give higher ratings of valence, consonance, and preference to all chord types in general. This result illustrates that affective reactions to music remain complex and multifaceted. As stated above, consonance-dissonance is a continuum rather than a dichotomy. In order to investigate consonance-dissonance in experimental studies, it is often simplified as the two extremities of the continuum. The investigations of Lahdelma and Eerola (2016) demonstrate that this is highly likely to give an oversimplified image of affective, cognitive, and neural processing of consonance-dissonance.

In light of the obtained findings on the effects of music training on dissonance processing it is notable that most studies examining musically experienced individuals focus on classical musicians instead of, for example, contemporary, jazz, or heavy musicians. The role of dissonance among music genres varies drastically. Presumably the affective responses to dissonance also vary among listeners and players of different music genres. However, to date, these differences have not been widely studied in neuroscience of music. On the other hand, a certain degree of universality or innateness may contribute to affective connotations of sensory consonance and dissonance in humans, based on findings in other species (e.g., Snowden & Teie, 2013), human infants (e.g., Masataka, 2006; Perani et al., 2010), and individuals from other music cultures (e.g., Fritz et al., 2009). In their recent review, Thompson and Balkwill (2010) describe the cue-redundancy model on cross-cultural music emotion perception (originally presented by Balkwill & Thompson, 1999). According to the model, affective connotations of for example sensory consonance vs. dissonance partly rely on psychophysical cues shared universally by humans. These cues are not specific to any music culture, but neither are they specific to music. This issue will be further discussed below.

DISCRIMINATING SENSORY CONSONANCE FROM DISSONANCE

Consonant and dissonant intervals are differentiated in low levels of the auditory nervous system: in the firing patterns of the auditory nerve (Bidelman & Heinz, 2011; Tramo et al., 2001), subcortical brainstem activity (Bidelman, & Krishnan, 2009), as well as cortical oscillatory activity in humans and even monkeys (Fishman et al., 2001). Different responses to them are observable also in auditory cortical activity, at the level of ERPs in Western listeners (Itoh, Suwazono, & Nakada, 2003,

2010; Minati et al., 2009; Regnault, Bigand, & Besson, 2001; Schön et al., 2005; Virtala et al., 2011). It seems likely that sensitivity to sensory consonance vs. dissonance is a biologically hardwired phenomenon, most likely not specific to humans (for a review, see Bidelman, 2013).

Consonance-dissonance categorization has indeed been observed behaviorally in other species, at least birds (Watanabe, Uozumi, & Tanaka, 2005) and monkeys (Izumi, 2000). A recent study showed that rats learned to discriminate between consonant and dissonant chords, but they could also learn to discriminate between different dissonant chords (Crespo-Bojorque, & Toro, 2015). Unlike humans, the rats could not generalize what they had learned to categorize novel chords as consonant vs. dissonant (Crespo-Bojorque & Toro, 2015; however Izumi, 2000, and Watanabe et al., 2005, demonstrated some generalization abilities in Java sparrows and monkeys). The results suggest that while rats may be able to learn to discriminate between dissonant and consonant chords, dissonance vs. consonance is not a relevant categorization for rats beyond any other learned chord categorization.

Among humans, consonance-dissonance categorization has been demonstrated already in infancy, as evidenced by auditory preference studies (Crowder et al., 1991; Masataka, 2006; Trainor & Heinmiller, 1998; Trainor et al., 2002; Zentner & Kagan, 1998), but as presented above, these results were recently compromised by Plantinga and Trehub (2014). Still, several behavioral findings suggest some discrimination of consonance from dissonance in 6- to 12-month-old Western infants (Schellenberg & Trainor, 1996; Trainor, 1997; Trainor & Trehub, 1993).

In the MMN study by Virtala and colleagues (2013), consonance-dissonance discrimination in triad chords was investigated in a controlled experimental setting in newborn infants. While root form major chords served as examples of highly consonant chords, the highly dissonant chord type introduced a minor second interval between the first two notes, followed by a tritone, both considered highly dissonant intervals (illustrated in Figure 1; Helmholtz, 1887/1954; Rossing et al., 2002). Newborn infants demonstrated readiness to discriminate between consonance and high levels of dissonance in chords at the level of the preattentive processing reflected by MMN (Virtala et al., 2013). Together with the results by Perani and colleagues (2010) on differential emotion-related brain activity patterns to consonant vs. dissonant music in newborns, this study offers by far the most conclusive evidence on

early sensitivity to sensory consonance-dissonance in Western newborns.

Comparisons of music cultures have been hesitant in naming musical universals. Still, many studies have reported superior processing and higher prevalence of small-integer compared to large-integer frequency ratios in music intervals in a large proportion of world's music cultures (Higgins, 2006; Stevens & Byron, 2009; Trehub, 2000). On the other hand, use of dissonant harmonic intervals is also seen in various music cultures (Brown & Jordania, 2011). Furthermore, spectral similarity to a harmonic series in consonant intervals, as pointed out by McDermott and colleagues (2010), further links human preference of consonance to preference for intervals that resemble natural sounds and, for example, vocalizations (see Gill & Purves, 2009). This suggestion is in line with the above-reviewed literature on major-minor processing.

The effects of musicianship on sensory consonance-dissonance processing in the brain have been reviewed by Bidelman (2013). Importantly, facilitated processing in musically trained individuals is seen already in the subcortical brainstem level (Bidelman, Krishnan, & Gandoun, 2011; Lee, Skoe, Kraus, & Ashley, 2009). In several ERP studies, responses to consonant and dissonant chords differed in both musicians and laymen, but musicians demonstrated larger differences than non-musicians or the response pattern differed between groups (Minati et al., 2009; Regnault et al., 2001; Schön et al., 2005). However, the results vary a lot between studies for no obvious reason. All of these studies are conducted in attentive listening conditions where participants have a task to rate the perceived pleasantness or consonance of the stimuli. It is difficult to tell apart affective and cognitive processes. More recently, Itoh and colleagues (2010) conducted an ERP study on processing consonant vs. dissonant intervals in a passive listening (ignore) condition. They found that consonance of the intervals affected the N2 response in musicians only.

To conclude, sensitivity to sensory consonance vs. dissonance is present in humans and non-human species in the low levels of the auditory system (Bidelman, 2013), evident already in newborn infants (Perani et al., 2010; Virtala et al., 2013). Higher prevalence of small-integer than large-integer frequency ratios, associated with sensory consonance vs. dissonance, is seen in world's music cultures (Higgins, 2006; Stevens & Byron, 2009; Trehub, 2000). These findings strongly suggest that it is a profound psychoacoustic phenomenon and serves as a biological predisposition to music (see Hannon & Trainor, 2007).

Conclusions

The main questions in the scope of this review were: 1) what the neurobiological basis and psychoacoustic origin of major-minor and consonance-dissonance is, and 2) how development, musical enculturation, and music training/expertise modify their affective and cognitive processing. In our view, sensory and affective processing of major-minor and particularly consonance-dissonance are present early in development and it is possible that their affective connotations have partly universal, biologically hardwired origins, presumably related to human vocalizations. Brain maturation, musical enculturation, as well as music training still significantly modulate their sensory and affective processing. In musicians, neural and behavioral categorization of major-minor and consonance-dissonance are more accurate than in non-musicians, and a significant proportion of this group difference is attributable to training effects.

When the (affective) music processing of small infants and children is studied, limitations set by their level of brain maturation and general affective processing should be acknowledged. Psychophysiological and brain measures can offer information on affective and cognitive responses to music in infants and small children and allow cross-cultural comparisons. While behavioral studies often can present more natural stimuli than highly controlled brain studies, neuroscientific experiments also have administered increasingly natural paradigms during the recent decade. Also, in future research, it would be important to make cross-cultural comparisons within the Western world; namely, to compare individuals with highly different musical preferences and backgrounds in terms of genre and time period (for genre comparisons, see Tervaniemi, Janhunen, Kruck, Putkinen, & Huottilainen, 2015; Vuust et al., 2012). A careful examination of music background is needed in these studies (for suggestions, see Gold, Frank, Bogert, & Brattico, 2013; Müllensiefen, Gingras, Musil, & Stewart, 2014). While major-minor and consonance-dissonance have a stereotypical, pronounced role in Western popular music, they are likely to be processed highly differently by, for example, players and listeners of heavy music, jazz, or early music. Also, in studies on small infants, their musical history also in terms of the prenatal period should be taken into account. This means carefully interviewing the parents on their musical activities and auditory environment during particularly the last trimester of pregnancy.

Innateness of a musically relevant categorization depends on the degree of sensory/acoustical differences

between the sounds. The discrimination between sensory consonance vs. dissonance can be made by human newborns (Perani et al., 2010; Virtala et al., 2013) as well as other species (Izumi, 2000; Watanabe et al., 2005), and it is rooted in the low levels of the auditory nervous system (Bidelman, 2013; Bidelman & Heinz, 2011; Bidelman & Krishnan, 2009; Tramo et al., 2001). The major-minor dichotomy, on the other hand, is less evident in infants (Crowder et al., 1991; Virtala et al., 2013), and cross-cultural and cross-species evidence is lacking. This dichotomy is also acoustically less obvious than the consonance-dissonance difference. In light of the cue-redundancy model of Balkwill and Thompson (1999), it is probable that the less there are sensory/acoustical differences between sounds, the larger is the role of nurture (exposure/training) in their processing. This view is supported by results by Virtala and colleagues (2013, 2014): the very small acoustical difference between a root major chord and an inverted major chord (second inversion) was discriminable to expert musicians but much less so to Western nonmusicians or newborn infants.

Based on the reviewed research, we suggest that in line with the cue-redundancy model of music emotions (Balkwill & Thompson, 1999), and the empirical evidence reviewed by Thompson and Balkwill (2010), psychophysical cues not specific to music can explain the partly universal origins of the affective connotations of consonance vs. dissonance *and also* major vs. minor. These cues are likely shared by major-minor and consonance-dissonance, as well as by music and speech (for a related review, see Juslin & Laukka, 2003). Also, we suggest that sensory consonance-dissonance categorization has a more profound universal basis than major-minor due to larger amount of these psychophysical cues; that is, a larger sensory/acoustical difference between them. Accordingly, (affective) major-minor processing is more strongly guided by cultural influences than sensory consonance-dissonance processing.

When reading the conclusions on the above-reviewed work, it should however be noted that they are written in the context of Western music only. The reviewed findings and presented arguments cannot take a stand on whether the Western music categorizations under interest are more natural, universal, or biologically hardwired than some other stimulus categories in Western or other music cultures. All music cultures are human-made and thus rely on the same basic properties of human auditory system. It is highly likely, although currently not known, that central categorizations and their affective labels in all music cultures have some universal components that relate to their psychoacoustic features.

In the end, all perceptual abilities, even if elementary and biologically hardwired, are modified by experience (nurture). For example musicianship and music training can facilitate the processing of the most basic elements of sound (Pantev & Herholz, 2011), as well as the neural representations of Western music chord types (Virtala et al., 2012, 2014). Vice versa, all culturally relevant conceptions of sounds, like chords in music or phonemes in language, build on basic properties of the human auditory system. Thus, they are always rooted in our biology.

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